# PLASTICITY AND POLYMORPHISM IN SEED GERMINATION OF *MIMULUS GUTTATUS* (SCROPHULARIACEAE)

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Abstract.— Seeds of 12 populations of *Mimulus guttatus* representative of the Wasatch Mountain ecotype were incubated for 17 months (one natural season plus a year) in five artificial climates found in phytotron studies to be important to the growth of the plants of that form of monkey flower. In all but the coldest climate, germination occurred promptly (3–8 days, on average), peaked during the first three weeks, and then tapered off gradually well into the second season. Generally, the amount and timing of germination was plastic, showing much the same range of responses in widely different climates both overall and for individual populations. However, in some cases, there were significant differences between populations indicative of polymorphism within the species. For example, germination was significantly slower, more variable, and less in amount the higher the elevation of origin of the populations. The responses of the population suggest the presence of both much plasticity and much polymorphism for germination characteristics in this form of *M. guttatus*.

The purpose of this investigation is to study seed germination in the yellow Monkey flower, *Mimulus guttatus* Fischer ex DC., in greater depth than was possible in the earlier surveys (Vickery 1963, 1967). In those surveys small samples of a series of species and varieties of *Mimulus* were studied in a broad range of artificial climates. The present study concentrates on the Wasatch ecotype of *Mimulus guttatus* (Vickery 1978) and on five artificial climates found in phytotron studies to be important for the growth of *M. guttatus* (Vickery 1972, 1974).

## Materials and Methods

Seeds from 12 populations of *M. guttatus* were collected for the study from the Wasatch mountain area of northern Utah and southern Idaho (Table 1). The experiments were carried out in four laboratory artificial climates and one greenhouse climate (Table 2). The seeds were germinated on moist blotters in petri dishes. Samples of 500 seeds, 125 per petri dish, were used for each population in each climate. The climates included extremes of the earlier studies (1 and 5), optimal and suboptimal growth conditions (3 and 4, respectively), and the contrasts of fluctuating and steady temperatures (1 and 2 vs. 3, 4, and 5). Germination was scored for 17 months, that is, through the 5-month germination season normal for *M. guttatus* in the Wasatch Mountains plus an additional year.

## Results and Discussion

Overall, germination in the four warmer climates (2–5), started as early as the third

Table 1. Origins of the populations of *Mimulus guttatus* studied, arranged by culture number, locality, and elevation.

| *M. guttatus* Fischer ex DC., n = 14 | |
|---|---|
| 5839 | Spruces, Big Cottonwood Canyon, Salt Lake Co., Utah, 2350 m. |
| 7273 | Draper, Salt Lake Valley, Salt Lake Co., Utah, 1390 m. |
| 7274 | Gorgoza Ranch, Parley's Summit, Summit Co., Utah, 1910 m. |
| 7311 | Fish Haven, Bear Lake, Bear Lake Co., Idaho, 2030 m. |
| 7312 | Rick's Springs, Logan Canyon, Cache Co., Utah, 2000 m. |
| 7314 | East Canyon, Salt Lake Co., Utah, 2060 m. |
| 7315 | Thousand Springs, Mill Creek Canyon, Salt Lake Co., Utah, 2215 m. |
| 7316 | Mill F East, Big Cottonwood Canyon, Salt Lake Co., Utah, 2670 m. |
| 7317 | Brighton, Big Cottonwood Canyon, Salt Lake Co., Utah, 2645 m. |
| 7318 | Homestead, Heber Valley, Wasatch Co., Utah, 1570 m. |
| 7319 | Snow Pine, Alta, Little Cottonwood Canyon, Salt Lake Co., Utah, 2710 m. |
| 11157 | Mill D North, Big Cottonwood Canyon, Salt Lake Co., Utah, 2520 m. |

Note: The experiments were carried out at the University of Utah, elev. 1500 m, near the center of the study area.

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TABLE 2. Experimental climates used for the seed germination study.

| | |
|---|---|
| 1 | Steady 4 C day and night, no photoperiod |
| 2 | Steady 25 C day and night, no photoperiod |
| 3 | Gradually changing from 4 C night to 17 C day, 16-hour photoperiod |
| 4 | Gradually changing from 14 C night to 17C day, 16-hour photoperiod |
| 5 | Standard greenhouse, changing from 10 C nights on average to 30 C days on average, 16-hour photoperiod. |

NOTE: Artificial climates 1 and 2 employed incubators, whereas climates 3 and 4 employed growth chambers programmed to rise and fall like natural July climates in the Wasatch Mountains (Dept. of Commerce, Climatological Data, 1971–1980).

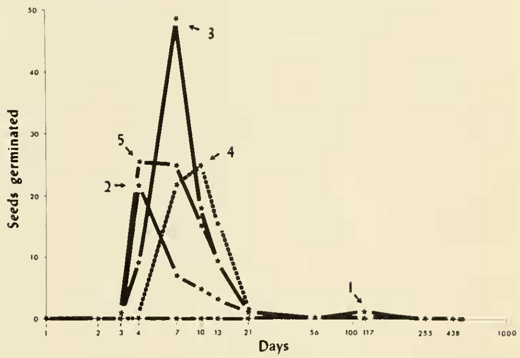


Fig. 1. The average number of seeds of all 12 populations of *M. guttatus* that germinated per day (Table 3) for each of the five climates studied (full data available on request). Peak germination occurred on day 7 in climate 3 with an average of close to 50 of the 500 seeds studied per population per climate germinating that day. The germination rate dropped off to approximately one seed germinating per 25,000 seeds per day by day 255 and to one-tenth of that rate by day 512, the end of the experiment.

day, peaked during the following week, tapered off to a low level by the end of the third week, but continued to occur occasionally well into the next year, forming a typical (Went 1957, Vegis 1963) leptokurtic curve (Fig. 1). Despite the overall pattern, germination varied noticeably from climate to climate in both speed and amount (Table 3) as Stakanov (1976) observed in similar studies on beans. For example, in the 17/14 C climate (4), the monkey flower seeds were significantly slower than in the other cliamtes both in starting to germinate and in achieving 50 percent of the ultimate, total germination for the 17-month trial period (Table 4). The slowing effect on germination of the suboptimal, 17/14 C climate parallels the striking reduction in plant growth observed in that climate in the phytotron (Vickery 1972, 1974) and suggests that the posited cause, too similar day and night temperatures, acts on speed of germination as well as plant growth. In fact, if the temperature is constant as in climate 2, total germination is significantly less than in the fluctuating climates, 3, 4, 5 (Table 4). Overall, the variable, but generally similar ranges of germination results in the four diverse, warmer climates suggest wide plasticity of response in *M. guttatus*.

In the cold, steady 4 C climate (1), in sharp contrast to the pattern of early germination in the four warmer climates, no germination occurred at all during the first four weeks (Fig. 1). After that, apparently the cumulative effect of the time spent at room temperature while the seeds were being watered and scored triggered a little germination—2 or 3 seedlings per petri dish—followed by a spurt of germination when the watering and scoring time was inadvertently prolonged. Thus, the latter data for climate 1 are ambiguous and were not analyzed. However, the early results are clear and are consonant with the extremely slow growth of the young plants in the steady 4 C climate of the phytotron (Vickery 1972, 1974).

In general, the 12 individual populations of *M. guttatus* exhibit statistically similar ranges of germination responses to the test climates (Table 5) with some apparent differences (Table 2, 5), much as Wright (1978, 1980) observed in *Panicum*. The differences range from slight and insignificant to moderate to three cases in which they are so pronounced as to be statistically significant (Table 5). On one hand, the overall similarities suggest a wide plasticity of the populations of response. On the other hand, the differences appear to reflect underlying genetic differences—polymorphisms—of the populations.

The germination results of the 12 populations correlate with the elevation of origin of the populations (Table 6). The populations show significantly longer times to first germination and to 50 percent germination as well as less total germination with increasing elevation. This is true not only overall but in most of the individual climates as well (Table 6). The variances of the overall times to first germination are also significantly greater the higher the elevation of origin (Table 6). The

TABLE 3. Germination results for four replicates of each of the 12 populations of *M. guttatus* in each of the four warmer climates (Table 2). Climate 1, steady 4 C, was omitted due to the ambiguity of the later results.

| Population | Climate | Days to first germination | Days to 50% germination | Total germination |
|---|---|---|---|---|
| 5839 | 2 | 5.25 ± 2.50 | 15.00 ± 9.90 | 34.75 ± 16.38 |
| Spruces | 3 | 5.00 ± 1.41 | 8.00 ± 1.83 | 81.50 ± 51.45 |
| | 4 | 8.00 ± 1.41 | 13.50 ± 2.08 | 73.25 ± 11.38 |
| | 5 | 5.00 ± 1.82 | 11.00 ± 0.82 | 52.25 ± 15.84 |
| | Average | 5.81 ± 2.10 | 11.90 ± 5.37 | 60.44 ± 31.86 |
| 7273 | 2 | 4.00 ± 0.00 | 5.75 ± 0.96 | 56.25 ± 13.77 |
| Draper | 3 | 5.00 ± 0.00 | 6.50 ± 0.58 | 63.50 ± 16.09 |
| | 4 | 6.00 ± 0.82 | 8.50 ± 0.58 | 68.00 ± 41.29 |
| | 5 | 4.50 ± 0.58 | 6.50 ± 1.00 | 86.25 ± 34.60 |
| | Average | 4.88 ± 0.89 | 6.81 ± 1.28 | 68.50 ± 28.30 |
| 7274 | 2 | 4.00 ± 0.00 | 14.75 ± 13.10 | 24.75 ± 6.95 |
| Gorgoza | 3 | 4.25 ± 0.50 | 6.50 ± 1.00 | 109.00 ± 36.21 |
| | 4 | 5.75 ± 0.96 | 10.25 ± 2.50 | 98.75 ± 20.37 |
| | 5 | 4.00 ± 0.00 | 6.00 ± 1.15 | 95.75 ± 23.16 |
| | Average | 4.50 ± 0.89 | 9.38 ± 7.03 | 82.06 ± 40.69 |
| 7311 | 2 | 6.33 ± 0.00 | 6.25 ± 0.50 | 65.50 ± 15.20 |
| Bear Lake | 3 | 5.25 ± 0.00 | 6.25 ± 0.50 | 102.75 ± 22.88 |
| | 4 | 7.75 ± 0.58 | 8.75 ± 1.26 | 78.00 ± 23.85 |
| | 5 | 5.00 ± 0.50 | 6.50 ± 1.00 | 90.25 ± 9.18 |
| | Average | 6.08 ± 0.73 | 6.94 ± 1.34 | 84.13 ± 22.06 |
| 7312 | 2 | 6.33 ± 2.31 | 6.50 ± 3.69 | 2.67 ± 1.41 |
| Logan Canyon | 3 | 5.25 ± 0.50 | 10.00 ± 0.82 | 79.25 ± 6.45 |
| | 4 | 7.75 ± 0.96 | 12.75 ± 0.50 | 21.25 ± 16.19 |
| | 5 | 5.00 ± 1.41 | 14.00 ± 4.24 | 67.25 ± 6.85 |
| | Average | 6.08 ± 1.67 | 10.81 ± 4.47 | 55.11 ± 32.97 |
| 7314 | 2 | 4.00 ± 0.00 | 10.50 ± 2.65 | 31.50 ± 7.85 |
| East Canyon | 3 | 6.00 ± 1.41 | 8.00 ± 2.71 | 88.75 ± 35.88 |
| | 4 | 5.25 ± 0.50 | 9.50 ± 1.29 | 98.00 ± 10.86 |
| | 5 | 4.75 ± 0.50 | 8.00 ± 2.16 | 97.75 ± 11.35 |
| | Average | 5.00 ± 1.03 | 9.00 ± 2.31 | 79.00 ± 33.21 |
| 7315 | 2 | 4.25 ± 0.50 | 8.25 ± 2.22 | 15.25 ± 2.36 |
| 1000 Springs | 3 | 6.00 ± 0.00 | 9.50 ± 0.58 | 68.72 ± 7.50 |
| | 4 | 7.00 ± 0.82 | 16.50 ± 7.59 | 77.75 ± 23.21 |
| | 5 | 5.00 ± 0.00 | 10.50 ± 1.00 | 59.00 ± 17.15 |
| | Average | 5.56 ± 1.15 | 11.19 ± 4.85 | 55.19 ± 28.24 |
| 7316 | 2 | 8.00 ± 2.16 | 17.25 ± 8.34 | 17.50 ± 9.61 |
| Mill Creek | 3 | 6.00 ± 0.82 | 22.50 ± 12.40 | 60.50 ± 28.18 |
| East | 4 | 9.50 ± 1.73 | 32.00 ± 4.32 | 49.25 ± 7.89 |
| | 5 | 8.50 ± 2.52 | 13.50 ± 2.38 | 34.00 ± 10.95 |
| | Average | 8.00 ± 2.16 | 21.31 ± 10.10 | 40.31 ± 22.19 |
| 7317 | 2 | 7.25 ± 2.63 | 10.50 ± 2.38 | 8.75 ± 7.59 |
| Brighton | 3 | 5.25 ± 0.50 | 10.50 ± 1.73 | 47.75 ± 8.66 |
| | 4 | 7.50 ± 0.58 | 12.50 ± 1.00 | 61.50 ± 6.66 |
| | 5 | 6.50 ± 1.00 | 9.25 ± 2.06 | 35.75 ± 9.54 |
| | Average | 6.63 ± 1.59 | 10.69 ± 2.06 | 38.43 ± 21.34 |
| 7318 | 2 | 3.25 ± 0.50 | 5.00 ± 0.00 | 65.25 ± 9.43 |
| Homestead | 3 | 4.25 ± 0.50 | 6.25 ± 0.50 | 85.00 ± 7.44 |
| | 4 | 6.75 ± 0.50 | 9.75 ± 0.50 | 74.50 ± 19.16 |
| | 5 | 5.00 ± 0.00 | 5.50 ± 1.00 | 80.25 ± 14.22 |
| | Average | 4.81 ± 1.38 | 6.63 ± 2.00 | 76.25 ± 14.16 |
| 7319 | 2 | 16.00 ± 10.74 | 16.75 ± 10.20 | 3.25 ± 1.21 |
| Alta | 3 | 7.25 ± 0.96 | 15.75 ± 12.30 | 8.50 ± 4.65 |
| | 4 | 11.75 ± 1.26 | 15.00 ± 5.35 | 8.50 ± 3.70 |
| | 5 | 8.50 ± 1.91 | 11.50 ± 0.58 | 9.00 ± 3.74 |
| | Average | 10.88 ± 6.04 | 14.75 ± 7.82 | 7.31 ± 4.05 |
| 11,157 | 2 | 3.75 ± 0.50 | 5.00 ± 0.00 | 82.00 ± 26.99 |
| Mill D | 3 | 5.25 ± 0.50 | 6.00 ± 0.00 | 97.25 ± 10.34 |
| North | 4 | 7.50 ± 1.73 | 11.75 ± 1.71 | 75.25 ± 9.00 |
| | 5 | 4.75 ± 0.50 | 5.00 ± 0.00 | 77.00 ± 22.69 |
| | Average | 5.31 ± 1.66 | 6.94 ± 3.00 | 83.00 ± 19.09 |
| All | 2 | 5.71 ± 4.60 | 9.98 ± 7.25 | 33.90 ± 28.32 |
| populations | 3 | 5.29 ± 1.11 | 9.65 ± 6.56 | 74.38 ± 34.14 |
| | 4 | 7.35 ± 2.02 | 13.40 ± 6.77 | 69.54 ± 28.18 |
| | 5 | 5.52 ± 1.80 | 8.94 ± 3.42 | 65.38 ± 30.94 |

TABLE 4. Comparison of germination in the different artificial climates. Climates that are underlined together are statistically inseparable according to the Student, Newman, Keuls Multiple Range Test (Woolf 1968). average values are given below the lines.

| | | | | |
|---|---|---|---|---|
| Days to 1st germination | 3 | 5 | 2 | 4 |
| | 5.3 | 5.5 | 5.8 | 7.4 |
| Days to 50% germination | 5 | 3 | 2 | 4 |
| | 8.9 | 9.6 | 10.2 | 13.4 |
| Total germination (Av. per petri dish) | 2 | 5 | 4 | 3 |
| | 34.6 | 65.4 | 69.5 | 74.4 |

slower and more varied germination responses seem a reasonable adaptation to the increasing unpredictability of the climate with increasing elevation in the Wasatch area (Department of Commerce, Climatological Data, 1971–1980). This finding of decreased germination is compatible, also, with my field observations that the populations appear to rely more on rhizomes than on seeds at higher elevations, i.e., there appears to be a cline of decreasing r-selection and increasing K-selection with increasing elevation.

Although the great majority of seeds germinated promptly during the first season in the four warmer artificial climates, a few, about 1 percent on average, in each of the populations did not germinate until the following season (Fig. 1). This result parallels the germination response of *M. guttatus* in the Wasatch Mountains. There, most of the seeds germinate soon after shedding, i.e., during the later part of the summer. They do not require an after-ripening period as many species do (Mayer and Poljakoff-Mayber 1975). They continue to germinate in decreasing numbers well into the fall. The seedlings overwinter as small (1–2 cm) rosette stage plants. A few new seedlings appear in the spring along the streams as new habitats are exposed with receding water levels. The late germinating seeds appear to constitute small but important seed banks (Harper 1977), both for springtime germination and for the survival of the populations in unfavorable years.

TABLE 5. Comparison of germination of the various populations. Populations within underlined groups are statistically inseparable, whereas populations in nonoverlapping groups are statistically distinct according to the Student, Newman, Keuls Multiple Range Test (Woolf 1968). Population culture numbers (Table 1) are given above the lines and average values for each population below the line.

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Days to first germination | 7274 | 7311 | 7318 | 7273 | 7314 | 11157 | 7315 | 5839 | 7312 | 7317 | |
| | 4.5 | 4.6 | 4.8 | 4.9 | 5.0 | 5.3 | 5.6 | 5.8 | 6.1 | 6.6 | |
| | | | | | | | | | | 7317 | 7316 |
| | | | | | | | | | | 6.6 | 8.0 |
| | | | | | | | | | | | 7319 |
| | | | | | | | | | | | 10.9 |
| Days to 50% germination | 7318 | 7273 | 7311 | 11157 | 7314 | 7274 | 7317 | 7312 | 7315 | | |
| | 6.6 | 6.8 | 6.9 | 6.9 | 9.0 | 9.4 | 10.7 | 10.8 | 11.2 | | |
| | | | | | | 7274 | 7317 | 7312 | 7315 | 5839 | 7319 |
| | | | | | | 9.4 | 10.7 | 10.8 | 11.2 | 11.9 | 14.8 |
| | | | | | | | | | | | 7316 |
| | | | | | | | | | | | 21.3 |
| Average total germination | 7319 | | | | | | | | | | |
| | 7.3 | | | | | | | | | | |
| | | 7317 | 7316 | 7315 | 7312 | 5839 | | | | | |
| | | 38.4 | 40.3 | 55.2 | 58.6 | 60.4 | | | | | |
| | | | | 7315 | 7312 | 5839 | 7273 | 7318 | 7314 | 7274 | 11157 | 7311 |
| | | | | 55.2 | 58.6 | 60.4 | 68.5 | 76.3 | 79.0 | 82.1 | 83.0 | 84.1 |

TABLE 6. Regression analysis of seed germination in the artificial climates versus elevation of origin of the population, given as F-ratio and p value. Significant values are underlined.

| Climates | First germination F = p = | 50% germination F = p = | Total germination F = p = |
|---|---|---|---|
| 2 | 11.462, .007 | 5.520, .041 | 2.444, .149 |
| 3 | 7.667, .019 | 7.942, .018 | 4.946, .050 |
| 4 | 16.586, .002 | 4.434, .061 | 6.894, .025 |
| 5 | 16.599, .002 | 2.767, .127 | 19.650, .001 |
| All together | 11.096, .007 | 7.649, .019 | 7.112, .024 |
| Standard deviation (all) | 6.168, .032 | 4.265, .066 | 2.578, .139 |

The Wasatch ecotype of *Mimulus guttatus* exhibits both much plasticity in the overall similarity of its range of seed germination responses to widely different climates and some apparent genetic polymorphisms for speed and amount of germination during the first season, for the speed and amount of germination in populations with different elevations of origin and for the ability to delay germination until the second season. Thus, the ecotype appear to be well adapted for survival in its climatically unpredictable area.

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